Geographic location, local environment, and individual size mediate the effects of climate warming and neighbors on a benefactor plant

Jesús Villellas[1,3,4], María B. García[2], William F. Morris[1]

[1] Biology Department, Duke University. 125 Science Dr., Durham, NC 27708, USA.

[2] Pyrenean Institute of Ecology (IPE-CSIC). Avda. Montañana 1005, Apdo. 13034, 50080 Zaragoza, Spain.

[3] Current address: Departamento Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales, MNCN-CSIC, E-28006 Madrid, Spain.

[4] Corresponding author: jesus.villellas@gmail.com. Telephone: 0034914111328.

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WFM conceived the study and JV and MBG set up the experiment. JV monitored the plants and performed data analysis. JV wrote the manuscript with help from WFM and MBG.

Abstract

Predictions of plant responses to global warming frequently ignore biotic interactions and intraspecific variation across geographical ranges. Benefactor species play an important role in plant communities by protecting other taxa from harsh environments, but the combined effects of warming and beneficiary species on their performance have been largely unexamined. We analyzed the joint effects of elevated temperature and neighbor removal on the benefactor plant *Silene acaulis*, in factorial experiments near its low- and high-latitude range limits in Europe. We recorded growth, probability of reproduction and fruit set during three years. The effects of enhanced temperature were positive near the northern limit and negative in the south for some performance measures. This pattern was stronger in the presence of neighbors, possibly due to differential thermal tolerances between *S. acaulis* and beneficiary species in each location. Neighbors generally had a negative or null impact on *S. acaulis*, in agreement with previous reviews of overall effects of plant-plant interactions on benefactors. However, small *S. acaulis* individuals in the north showed higher growth when surrounded by neighbors. Finally, the local habitat within each location influenced some effects of experimental treatments. Overall, we show that plant responses to rising temperatures may strongly depend on their position within the geographic range, and on species interactions. Our results also highlight the need to consider features of the interacting taxa, such as whether they are benefactor species, as well as local-scale environmental variation, to predict the joint effects of global warming and biotic interactions on species and communities.

Keywords

Arctic-alpine communities; distribution range limits; global warming; plant-plant interactions; stress gradient hypothesis

Introduction

Ongoing anthropogenic climate change is significantly affecting plant performance, for example by modifying growth and reproduction (Myneni et al. 1997; Sala et al. 2000; Walther et al. 2002) and shifting the geographical ranges of some species (Parmesan and Yohe 2003). Its consequences on populations may differ across a species' range (O'Neill et al. 2008; Doak and Morris 2010), but such intraspecific variation is frequently overlooked in assessments of climate change effects. Another important shortcoming when predicting responses to global warming is the neglect of biotic interactions (Adler et al 2012; Cavieres et al. 2014; Ehrlén and Morris 2015; Valladares et al. 2015). Interactions between species can have a profound direct effect on their performance, and also mediate the effects of environmental changes (Davis et al. 1998; Brooker 2006). Moreover, the impact of biotic interactions on the performance of a focal species may also differ across its geographical range (Doxford et al. 2013, Louthan et al. 2018). For example, the stress gradient hypothesis posits that neighboring plants will be competitors at the more benign end of a stress gradient, but benefactors at the more stressful end of the gradient (Bertness and Callaway 1994). This hypothesis was first tested on altitudinal gradients (e.g. Choler et al. 2001; Callaway et al. 2002), but an equivalent gradient across latitude may also influence the joint effect of global warming and biotic interactions on plant performance (Bertness and Ewanchuk 2002; Anthelme et al. 2014). For example, warming could exacerbate competition at more benign low latitudes but reduce abiotic stress and thus facilitation at high latitudes (Klanderud 2005; Klanderud and Totland 2005; Anthelme et al. 2014; but see Cavieres and Sierra-Almeida 2012).

However, predicting the combined effects of climate warming and neighbors on a focal species at its low- and high-latitude range limits may require us to account for some complicating factors. First, whether interactions with neighbors decrease or increase the performance of a focal species may depend on the ecological role played by that species (Butterfield 2009). While many studies have analyzed the effects of biotic interactions on beneficiary plants (i.e., those

54 that are facilitated by benefactor species; see references in Callaway 2007; Soliveres et al.
55 2015), there is much less information on the consequences of these interactions for benefactors
56 (Bronstein 2009; Schöb et al. 2014), despite their pivotal role in supporting diversity in their
57 communities. The evidence that does exist suggests that the net effects of beneficiary plants on
58 the benefactors are predominantly negative (McIntire 2014; Schöb et al. 2014; Michalet et al.
59 2016; but see García et al. 2016), probably because benefactors are already adapted to stressful
60 conditions and cannot be facilitated by less-adapted neighbors (Butterfield 2009). Another
61 complicating factor is that co-occurring species may respond differently to warming (Gilman et
62 al. 2010), for example if their thermal niches differ. The effects of beneficiary species on the
63 benefactor will thus depend on their relative responses to warming. In Fig. 1, we illustrate some
64 plausible ways these factors could result in complex responses to climate warming across the
65 latitudinal range of a benefactor plant. We assume that plant performance is a unimodal function
66 of temperature, falling off at temperatures both above and below an optimum range, as is often
67 observed (Doak and Morris 2010; Angert et al. 2011; Peterson et al. 2018). The direct effect of
68 global warming (i.e., in the absence of neighbors) would thus be negative at low latitudes (Fig.
69 1 a-c) but positive at high latitudes (Fig. 1 d-f). The presence of neighbors may have an
70 independent effect on performance (Fig. 1 a,d), or it may exacerbate (Fig. 1 b,f) or reverse (Fig.
71 1 c,e) the effects of elevated temperatures. These interactive effects will thus determine whether
72 the net effect of warming in the presence of neighbors is beneficial or detrimental.
73
74 Despite the complexity already apparent in Fig. 1, yet more factors can influence how global
75 warming and species interactions affect plant performance. Species responses may differ
76 depending on the size and ontogenetic phase of the individuals, or the vital rate being
77 considered (Soliveres et al. 2015). For example, younger or smaller plants may be more
78 vulnerable to climate change, but they may also be more likely to benefit from facilitation
79 (Miriti 2006), and García et al (2016) found contrasting effects of species interactions on
80 flowering and fruiting rates of a benefactor plant. Furthermore, in addition to large-scale
81 environmental gradients, variation in local conditions can also alter the effects of global climatic

trends (Kennedy 1997; Williams et al. 2008). Several studies have shown contrasting plant responses to temperature or rainfall manipulations, depending on local factors such as soil characteristics, level of grazing, or water stress (Liancourt et al. 2013; Spence et al. 2014; Eskelinen and Harrison 2015; Sharkhuu et al. 2016). Overall, if we want to address plant responses to global warming, we will need to consider the influences of interactive effects of neighbors, species' ecological roles and life cycles, non-linear responses to temperature, and the effects of the local environment across the geographical distribution.

Factorial experiments are a standard method to assess interactive effects of neighbors and either abiotic (Klanderud 2005; Klanderud and Totland 2005; Rixen and Mulder 2009) or biotic (Louthan et al. 2015) stressors on performance of a focal species. However, to our knowledge, such studies have never been performed simultaneously at both ends of the latitudinal range of a species to better evaluate potential range shifts. Here we report the results of a factorial experiment conducted over three years, in which we combined warming with neighbor removal near both the low- and high-latitude range limits of the benefactor cushion plant *Silene acaulis* (moss campion) in continental Europe. We analyzed the interactive effects of temperature and neighbor presence on plant performance, as well as intraspecific variation in response to these effects due to local environmental heterogeneity and individual size. Moreover, to have a more integrative view of the species' response, we considered effects of warming on both growth and reproduction. We expected overall negative effects of warming on plant performance in the south (where the species may already be near its upper thermal limit), but positive effects in the north (where it may be closer to its lower thermal limit). Given that *S. acaulis* is a benefactor (e.g., Molenda et al. 2012; Aubert et al. 2014), we expected a generally negative effect of neighbor presence in both regions, but recognized that different responses of neighbors to warming relative to that of *S. acaulis* could lead to different outcomes at the two extremes of the latitudinal range.

Methods

110

111 *Study species*

112 *Silene acaulis* (L.) Jacq. (Caryophyllaceae; "moss campion") is a long-lived perennial plant that
113 forms a low-growing cushion with a single taproot. The species is gynodioecious, with both
114 female and hermaphrodite individuals. Flowers are pollinated by insects. *S. acaulis* is found in
115 arctic and alpine tundra habitats throughout the northern hemisphere (Jones and Richards 1962).
116 In Europe, it is present from the high Arctic to the Pyrenees and the Apennine Mountains. The
117 study species has been found to facilitate the establishment of other species in different
118 boreoalpine habitats in N Europe and N America, although this facilitation effect may vary with
119 individual gender and abiotic stress (Antonsson et al 2009, Molenda et al. 2012, Cranston et al.
120 2012).

121

122 *Location and establishment of the experiment*

123 We conducted factorial experiments at the latitudinal extremes of the distribution of *S. acaulis*
124 in continental Europe to measure the separate and combined effects of elevated temperature and
125 neighbors on individual performance. The northern site, in the Latnjajaure valley in Swedish
126 Lapland (GPS coordinates: $68^0$21'N, $18^0$29'E; 1000 m.a.s.l.), has a mean annual temperature of
127 -2.0 ^{o}C and mean annual precipitation of 839 mm (Antonsson et al. 2009). The plant community
128 in the Swedish site is mainly composed of circumboreal and boreo-alpine vascular plants (e.g.,
129 *Carex vaginata*, *Festuca ovina*, *Cassiope tetragona*, *Thalictrum alpinum*, *Betula nana*,
130 *Calamagrostis lapponica*), mosses (e.g., *Hylocomium splendens, Dicranum groenlandicum,*
131 *Kiaeria starkei, Polytrichum juniperinum*) and lichens (e.g., *Cetraria* and *Cladina* species;
132 Molau and Alatalo 1998). The southern site is located in the Aisa valley in the Spanish Pyrenees
133 (GPS coordinates $42^0$43'N, $0^0$33'W; 2040-2105 m.a.s.l.). Its closest weather station (Aisa
134 village, ca. 8 km from the study site at 1100 m.a.s.l.) shows a mean annual temperature of 10°C
135 and mean annual precipitation of 1100 mm (García-Ruiz et al 1996). The plant community in
136 the Spanish site is composed of vascular species with different distributions (M.B. García, *pers.*
137 *obs.*; D. Gómez, *pers. comm.*): Mediterranean (e.g., *Koeleria vallesiana*, *Bupleurum*

ranunculoides, *Galium pyrenaicum*, *Sideritis hyssopifolia*), alpine from southern or central European mountains (e.g., *Festuca gautieri*, *Astragalus sempervirens*, *Anthyllis montana*, *Carduus carlinifolius*), boreoalpine (e.g., *Gentiana verna*) or wider (e.g., *Androsace villosa*). These species have lower altitudinal limits than the boreoalpine *S. acaulis*, most reaching altitudes below 1300 m.a.s.l. (whereas *S. acaulis* rarely occurs below 1800 m.a.s.l.; Atlas of Aragon Flora, http://floragon.ipe.csic.es/index.php).

Local-scale variation in environmental conditions can modify the demography of *S. acaulis* at both high and low latitudes (Morris and Doak 2005; Villellas et al. 2016). Thus, we located at each site of our study a more mesic area with higher vegetation cover (HC) and a drier area with lower vegetation cover (LC). These two areas were separated from each other by ca. 1 km in both sites. To characterize HC and LC locations, we used a visual estimate of vegetation cover (0-25, 25-50, 50-75 or 75-100% of total vegetation cover). All plots from HC habitats showed a vegetation cover of 75-100%, whereas plots from LC habitats showed a vegetation cover of 25-50%. In each site and habitat, we established permanent plots when the snow melted in 2013 (12 plots per habitat in the northern site, and in the southern site, 10 plots LC habitat and 14 in the HC habitat). In half of the plots per site and habitat, we installed hexagonal open-top chambers (OTCs) to increase temperature, leaving the other half at ambient temperature (control). OTCs were constructed following one of the standard designs of the International Tundra Experiment (ITEX; http://www.geog.ubc.ca/itex/). Specifically, they had fiberglass walls that admitted sunlight and open tops that admitted precipitation and pollinators, and were 2.08 m in diameter at the base and 0.58 m high, with sides inclined at 30 degrees. Control plots had a similar size as OTC plots.

In each plot, we identified all *S. acaulis* individuals with 20 or more branch tips that were separated by at least 10 cm from conspecifics (we did not consider individuals in the periphery of the chambers to minimize edge effects). Plots contained an average of 9 plants, for a total of 422 monitored individuals (218 in Sweden and 204 in Spain) in 48 plots. One half of the plants

within each plot were randomly assigned to have all neighboring plants within 10 cm from the edge of the focal plant clipped at the ground level, avoiding damage to *S. acaulis* roots or leaves. Neighboring plants growing within the cushion were also clipped where they emerged from the cushion. Clipping was repeated at the beginning and end of each growing season. Overall, the experiment included on average 53 plants in each of the four treatment combinations (OTC/control crossed with neighbor removal/presence) per site.

To measure the effect of the OTCs on surface soil temperature, we buried a small temperature logger (iButton; https://www.maximintegrated.com/en/products/digital/data-loggers/DS1921G.html) enclosed in a waterproof plastic vial just below the ground surface in 5 OTC and 5 control plots in each habitat in each site. iButtons registered temperature every 4 hr during three growing seasons (from late June to September in the Spain site, and from early July to late August in the Sweden site). At the end of the experiment, mean daily temperature during the growing season was found to be significantly higher in OTC than in control plots, according to a linear model including warming treatment, site, habitat, and year as fixed main effects (*lm* function, *stats* package, R Core Team 2017; $t = 4.31$, $p < 0.001$). OTCs increased temperature by 1.0 ± 0.08 ^{0}C (mean ± standard error) in Spain and 0.5 ± 0.21 ^{0}C in Sweden. We verified with likelihood ratio tests (*anova* function, *stats* package, R) that the addition of interactions between the warming treatment and either site ($p = 0.154$) or habitat ($p = 0.496$) did not significantly improve the fit of the model. The increase in air temperature just above ground is probably higher than the 0.5-1 ^{0}C we observed just below the ground surface, and lies at the low end of the range of air temperature increases obtained in previous OTC studies (Marion et al. 1997). OTCs were taken down during winter in Spain due to a high exposure to wind but were left in place in Sweden. Three (out of 12) OTCs in Spain were damaged after the first growing season and were not replaced for the following years (plants from those plots were thus only sampled in the first growing period).

Plant measurements

When we established the plots at the beginning of the first growing season, we marked each plant with a colored plastic toothpick. We also determined the area of their cushions (by measuring the major and minor axes, using the formula for an ellipse, and subtracting the area of that ellipse that was not living plant tissue; cf. Doak and Morris 2010). At the end of the growing season (late August – September) in 2013, 2014, and 2015, we recorded which plants were still alive, and, for live plants, the cushion area and the number of fruits produced that season.

We measured the effects of the OTC and neighbor removal treatments on three response variables: growth in size from the start to the end of the experiment, whether a plant produced fruits or not in a given year, and the number of fruits per cm^2 of cushion area per year (conditional on producing fruits). To reduce the impact of measurement error on our assessment of growth, we treated growth as a binary variable and considered any plant that increased in area by 5% or more to have grown. We assessed growth over the entire three year period because these tundra plants grow slowly. We only analyzed probability of reproduction and fruit production on female individuals, because hermaphrodites produced on average only one fifth as many fruits per unit area as did females (cf. Morris and Doak 1998), and showed no clear response to the warming or neighbor removal treatments in preliminary analyses. Across the two sites, an average of 90% of the plants survived to the end of the experiment, so we had little power to detect treatment effects on survival, and did not assess them.

Analyses of plant performance

We tested for effects of warming and neighbor removal treatments on plant performance in each site using generalized linear mixed models (GLMMs). The error distribution was set as binomial for the probability of growth and the probability of reproduction, and normal for number of fruits per unit area (hereafter "fecundity"). We constructed for each performance measure a full model with the fixed effects of: 1) warming treatment (control vs elevated temperature); 2) neighbor removal treatment (neighbors / no neighbors); 3) habitat (lower vs

higher vegetation cover); 4) focal plant size (log-transformed); and 5) two-way interactions between warming and neighbor treatments, and between each of them and both habitat and plant size (Table 1). Plant size was included in the analyses to avoid possible confounding effects, since cushions were larger in Spain (mean area = 226.67 cm^2; SE = 22.46 cm^2) than in Sweden (mean area = 189.64 cm^2; SE = 17.35 cm^2). There were no differences in mean plant size between habitats within each site. More complex models with three-way interactions did not show additional significant effects in a preliminary analysis, and are not shown. In the analyses of growth and reproduction, the full model also included a random effect of plot, but there were not enough reproductive individuals per plot to include a random effect of plot on fecundity. Additionally, in the analyses of reproduction and fecundity, the full model included a fixed effect of year and a random effect of individual.

To test the effects of warming and neighbor treatments, either alone or through interactions, we compared for each site and performance measure the full models with all possible models including subsets of the predictors (*MuMIn* package, R). Specifically, we searched for the model that provided the best fit to the data using the Akaike Information Criteria corrected for finite sample sizes (AICc; Burnham and Anderson 2003; Johnson and Omland 2004). When warming or neighbor removal treatments showed significant interactions with habitat in the optimum model, we repeated the analyses for each habitat separately. To evaluate the consistency of the best models, we selected the set of competing models with ΔAICc values < 2. We then calculated the weight for each effect in the full model, by summing the Akaike weights of the competing models in which they appear (Burnham and Anderson 2003). The weight for each effect can go from 1 (present in the best model and all the competing models) to 0 (not present in any model), and was used to compare the importance of the effects appearing in the best model to those not included. Finally, we calculated least-squares means of performance traits for warming and neighbor removal treatments (*lsmeans* function, *lsmeans* package, R).

Results

250

251 *Plant responses in Spain*

252 At the low-latitude site, the warming treatment had different effects on *S. acaulis* depending on
253 the measure of plant performance, whereas the effect of neighbor presence was always negative
254 or null (Fig. 2a-d, 3a-b). The effect of warming on growth differed between habitats (as
255 indicated by the Warming × Habitat interaction in the best model; Table 1): warming decreased
256 growth in the habitat with low vegetation cover, but had no effect in the habitat with high
257 vegetation cover (Fig. 2a-b). The impact of warming on the probability of reproduction
258 depended on the neighbor removal treatment (Warming × Neighbor interaction; Table 1),
259 turning from a positive effect in the absence of immediate neighbors to a negative effect in the
260 presence of immediate neighbors (Fig. 2c). The impact of warming on the probability of
261 reproduction also depended on plant size (Warming × Plant size interaction), and was negative
262 on small plants and weakly positive on large plants (Fig. 3a). Finally, the warming treatment did
263 not have any significant effect on fecundity (Fig. 2d). There was a negative effect of neighbor
264 presence on fecundity, which was more pronounced in the largest plants (Neighbor removal ×
265 Plant size interaction; Fig. 3c).

266

267 *Plant responses in Sweden*

268 At the high-latitude site, the effect of warming on *S. acaulis* also differed depending on the
269 performance measure and other factors (Fig. 2e-h). Warming had a positive effect on growth,
270 although the effect was weaker in the absence than in the presence of neighbors (Fig. 2e;
271 Warming × Neighbor interaction, Table 1). Reproduction was unaffected by the warming
272 treatment (Fig. 2f). The effect of warming on fruit production was different depending on the
273 habitat (Warming x Habitat interaction; Table 1): warming had a positive effect in the habitat
274 with high vegetation cover (Fig. 2h), but exerted no significant effect where vegetation cover
275 was low (Fig. 2g). The effect of neighbor presence was generally null or negative (Figs. 2e-h,
276 3b,d). Reproduction was affected by an interaction between neighbors and plant size, in which
277 neighbor presence was negative for smaller plants but had no effect on larger plants (Fig. 3d).

278 However, neighbors did have a positive effect on growth of small individuals (Fig. 3b; see
279 Neighbor × Plant size interactions in the best model in Table 1).
280
281 *Consistency of best models*
282 Results were in general very consistent across the set of competing models. In fact, the factors
283 found in the best models had an average weight of 0.92 of a possible 1.0 (Table 1), and showed
284 no important qualitative changes in their effects across competing models (Online Resource 1).
285 In contrast, the effects that were missing from the best model but which were present in any of
286 the other competing models showed on average a weight of 0.30, and always showed
287 confidence intervals overlapping zero. The estimates of the effects and *p*-values from the best
288 model in each set of analyses are also provided for further information (Online Resource 2).
289
290 **Discussion**
291
292 In our study, we addressed a critical gap in global warming studies by assessing experimentally
293 how increased temperature and species interactions will jointly affect plant performance across
294 a species' geographical range. We also aimed to shed light on the less studied effects of plant-
295 plant interactions on benefactors. The effects of experimental warming on the benefactor
296 cushion plant *S. acaulis* were positive at the northern limit and negative at the southern limit for
297 some performance measures, although this pattern was stronger in the presence than in the
298 absence of neighbors (Fig. 2c,e). In contrast, the effects of neighbors were in general negative or
299 null both in the northern and southern locations. Finally, the effects of warming and neighbors
300 also varied with the local habitat and the size of the cushion. Our study thus shows some general
301 patterns regarding the overall response of a benefactor plant to warming and biotic interactions,
302 but also highlights the influence of additional individual-level and environmental factors on the
303 consequences of these drivers.
304

The finding that warming had in general more negative effects in the southern location of this boreoalpine plant supports our hypothesis that southern populations are already experiencing ambient temperatures close to the species' upper thermal tolerance. In contrast, northern populations are exposed to colder temperatures, and experimental warming seems to improve some of their performance measures by ameliorating the thermal conditions they experience. Similarly, previous studies have predicted population declines at the southern limit for this (Doak and Morris 2010) and other (Lesica and McCune 2004) boreoalpine species if warming persists, whereas positive effects of enhanced temperature on *S. acaulis* have been found near the northern range edge (Alatalo and Totland 1997; but see Alatalo and Little 2014). However, the expected effects of warming in our experiment changed in some cases depending on the local conditions. In the southern location, the negative effect of enhanced temperature on growth disappeared in the local habitat with higher vegetation cover. The higher abundance of vegetation in the local community could have created or reflected more mesic and sheltered conditions that would allow *S. acaulis* to better cope with thermal stress. This suggests that the species thermal tolerance may be higher for some performance measures, such as growth, as long as water is abundant. Conversely, in the northern population, fruit production was not positively affected by warming when vegetation cover was low (Fig. 2g). Possibly, reduced water availability with higher temperatures hampers reproduction in such exposed conditions. OTCs could also partially alter water availability through rain exclusion or dew increase (Marion et al. 1997), although the large top of chambers used and belowground water diffusion probably minimize these effects. Soil water content - and how warming affects it - may be key for predicting species responses to global change (e.g., Giménez-Benavides et al. 2017), but such local effects should be confirmed by monitoring replicated habitats with controlled high and low water availability. Contrasting effects of experimental warming across local conditions have also been found in other plants in cold biomes (Liancourt et al. 2013; Spence et al. 2014; Sharkhuu et al. 2016), highlighting the relevance of fine-scale environmental information for evaluating species performance in these ecosystems.

The general pattern of positive effects of warming in the north and negative effects in the south was stronger when *S. acaulis* was surrounded by neighbors, indicating that the consequences of global warming and species interactions should not be evaluated alone (see also Davis et al. 1998; Brooker 2006; Cavieres et al. 2014). In our southern location, even though warming had a positive direct effect on reproduction, its net effect was negative when neighbors were present (Fig. 2c). This might be explained by a differential response to warming between the boreoalpine *S. acaulis* and some surrounding taxa with more Mediterranean or southern alpine distributions. For example, lower-altitude Poaceae and Fabaceae species may have benefitted more than the focal species from higher temperatures and become more competitive, a process known as thermophilization (Gottfried et al. 2012). The second interaction between warming and neighbor effects was found in the northern location, where the negative effect of neighbor competition on *S. acaulis* growth found under ambient temperature disappeared with warming. Mosses, which are abundant in this area (Molau and Alatalo 1998; J. Villellas, *pers. obs*), have been reported to suffer negative consequences of increased temperatures in previous experiments (Alatalo 1998, Hobbie et al 1999). If this phenomenon also took place in our warmed plots, a diminished competitive ability in mosses (or in other species with similar thermal tolerances) could explain the observed positive consequences for *S. acaulis*. This decrease in competition with an amelioration of the environment seems to contrast with expectations from the stress-gradient hypothesis and results from most previous studies (Shevtsova et al 1997; Klanderud 2005; Klanderud and Totland 2005; Rixen and Mulder 2009; but see Hobbie et al 1999; Cavieres and Sierra-Alemida 2012). However, this contrast is only apparent, since warming would not constitute an amelioration of the environment for mosses, only for *S. acaulis*. Our results in both southern and northern locations suggest that the joint effects of warming and biotic interactions may depend on the relative thermal tolerances of the interacting taxa (Hobbie et al 1999, Gilman et al. 2010). This could be particularly relevant when co-occurring species are located in different parts of their respective geographical distributions (e.g., central vs. peripheral; Brooker 2006). However, factorial experiments

360 analyzing the abundance and performance of both beneficiary and benefactor plants across
361 ranges will be needed to confirm this hypothesis.
362
363 Irrespective of warming treatment, the effect of neighbor presence was in general negative or
364 null both in the northern and southern localities, as we had expected for a benefactor cushion
365 plant. Moreover, for some performance measures, the effect of neighbors was more negative in
366 the local habitats with higher vegetation cover (Fig. 2a-b, g-h), probably because those
367 neighbors were also more abundant in HC than in LC habitats. Although both negative and
368 positive effects of beneficiary species on benefactors may be found (Cranston et al. 2012;
369 McIntire 2014), the net effects have been predominantly negative in previous studies (McIntire
370 2014; Schöb et al. 2014; Michalet et al. 2016). Our results thus support the view that community
371 role (being a benefactor) may be more important for the outcome of species interactions than
372 environmental conditions (Soliveres et al. 2015). In our study, we focused on the overall effects
373 of the beneficiary community on *S. acaulis*, and we assumed that this community included both
374 plants within *S. acaulis* cushions and those growing within a radius of 10 cm around. In the
375 future, additional experiments differentiating both types of neighbors would help to define in
376 more detail the components of the beneficiary community.
377
378 Individual plant size modified the effect of neighbors on *S. acaulis*, in agreement with previous
379 studies in both benefactor and beneficiary plants (Escudero et al. 2005; le Roux et al. 2013;
380 Nuche and Alados 2017). In fact, the only positive effect of neighbor presence found on *S.*
381 *acaulis* was on growth of small individuals in the northern location. When an interaction
382 between neighbors and plant size was detected in our study, the effect of neighbors was in
383 general more negative for larger plants (Fig. 3 b,c), possibly because they host a larger and more
384 diverse set of species within their cushions and thus receive more competition. However, in the
385 case of probability of reproduction in Sweden, the effect of neighbor presence was less harmful
386 in the largest plants (Fig. 3d). Competition may be counterbalanced by a higher attraction of
387 pollinators due to a higher flower abundance in the immediate vicinity, increasing the

388 probability of reproduction in a region where insect presence is probably lower than in the
389 south. Facilitation through pollinator attraction has been reported in other plant communities
390 (Hunter and Aarssen 1988; Ghazoul 2006).
391
392 That warming and neighbors do not always have consistent effects on growth and reproduction
393 highlights the importance of considering multiple demographic rates to evaluate plant responses
394 to global warming and biotic interactions (Arft et al. 1999; Goldberg et al. 1999). Maestre et al.
395 (2005) found that both the outcome of plant interactions and the effect of abiotic stress on that
396 outcome depended on the measure of performance. Contrasting responses of a benefactor plant
397 to species interactions have even been found for closely related reproductive measures, such as
398 flowering and fruiting rates (García et al 2016). In our experiment, the responses of growth and
399 reproduction differed not only across treatments, but also across habitats and plant sizes. As a
400 next step, population models that integrate the effects of the different vital rates (growth,
401 survival, reproduction and recruitment) will be needed to assess responses of the population
402 growth rate to biotic and abiotic drivers. For example, population models could help to evaluate
403 if the generally more negative effects of warming found in the southern location of *S. acaulis*,
404 especially in the presence of neighbors, will lead to a contraction at the species' southern range
405 margin in Europe, as has been suggested may occur in North America (Doak and Morris 2010).
406
407 In conclusion, the different patterns found in *S. acaulis* near the southern and northern limits
408 show that plant responses to rising temperatures may strongly depend on the location of
409 populations within species' ranges, but also on the influence of biotic interactions. We thus
410 advocate for refining predictions of global warming effects on plant performance by including
411 information both on species interrelations and geographic variation among populations, as
412 suggested previously (O'Neill et al. 2008; Ehrlén and Morris 2015; Valladares et al. 2015). Our
413 results also highlight the importance of the ecological roles of species for plant-plant
414 interactions. To our knowledge, this is the first study evaluating feedback effects of beneficiary
415 species in the southern and northern range limits of a benefactor, and the predominantly

negative impact detected agrees with previous reviews (Schöb et al. 2014). Finally, we found that additional factors, such as local-scale variation in environmental conditions, the size of individuals or the chosen measure of performance, influenced the results of our experiment. Overall, understanding the joint effects of global warming and species interactions on plant performance seems to be more complicated than choosing one of the possible scenarios proposed in the initial conceptual figure (Fig. 1), and will require integrative approaches that consider geographic, environmental and species-specific factors.

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Conflict of interest

The authors declare that they have no conflict of interest.

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627 **Figure legends**

628

629 **Fig. 1** Predicted combined effects of warming and neighbors on performance in a benefactor
630 cushion plant (other outcomes are possible). Neighbors are assumed to be competitors at
631 ambient temperature. In panels a-c), ambient temperature is at or above the optimum
632 temperature for the focal species (as might be typical near the low-latitude range limit). a)
633 Warming and neighbors decrease performance independently. b) Warming has direct negative
634 effects, which are exacerbated by the presence of neighbors (if they benefit from warming). c)
635 Warming has direct negative effects, but neighbor presence is only negative at ambient
636 temperature (if neighbors are more negatively affected by warming than the benefactor). In
637 panels d-f), ambient temperature is below the optimum temperature for the focal species (as
638 might be typical near the high-latitude range limit). d) Independent effects from warming
639 (positive) and neighbor presence (negative). e) Warming is beneficial in isolation, but the effect
640 is reversed in the presence of neighbors (competition is exacerbated due to more positive effects
641 of warming on neighbors than on the benefactor). f) Benefit from warming is enhanced by the
642 presence of neighbors (competition disappears if warming is less beneficial for neighbors than
643 for the benefactor). Color version of this figure is available online

644

645 **Fig. 2** Combined effects of warming and neighbor treatments on *Silene acaulis* performance in
646 Spain (left panels) and Sweden (right panels), according to best models. The three measures of
647 performance are a, b, e) probability of growing (% growth), c, f) probability of fruiting (%
648 reproduction;), and d, g, h) fruit production per unit area conditional on reproducing (Fruits cm^{-2}).
649 Plant performance at ambient (grey) and elevated (red) temperature is compared both in the
650 absence and presence of neighbors. Bars represent least-squares means ± standard errors,
651 maintaining the other factors present in the best models constant. Significant effects of warming
652 treatment (WT), neighbor treatment (NT), plant size (SZ), or the interactions among them
653 (WT×NT, WT×SZ, NT×SZ; see also Fig. 3), are indicated at the top-right corners of the panels.
654 When there is a significant interaction between habitat and either warming or neighbor

655 treatments (Table 1), plant performance is displayed separately for habitats with low (LC) and
656 high (HC) vegetation cover (a-b, g-h). Color version of this figure is available online
657
658 **Fig. 3** Combined effects of plant size and either warming or neighbor treatments on the
659 performance measures of *Silene acaulis*, according to best models. Plant performance is shown
660 for ambient (grey) and elevated (red) temperatures, or in the absence (grey) or presence (green)
661 of neighbors. Bars represent least-squares means (± standard errors) for individuals of the 0.05
662 (small), 0.5 (medium) and 0.95 (large) quantiles of the size distribution in each analysis,
663 maintaining the other factors present in the best models constant. Results are shown for Spain
664 (left panels) and Sweden (right panels). Color version of this figure is available online

Tables

Table 1. Full model for testing the effects of warming (WT) and neighbor (NT) treatments on three performance measures, and best model for each measure at each site according to the Akaike Information Criteria for limited sample sizes (AICc). The additional effects of habitat (HB), cushion size (SZ) and year (YR; only for reproduction and fecundity), and the two-way interactions of either WT or NT with HB or SZ, are also considered. The Akaike weight for each effect across competing models is shown in parentheses (see Methods for details). Additional analyses for LC and HC habitats separately are shown when WT or NT present significant interactions with habitat in main model

Performance measure	Site	Predictors
-	-	Full model: Performance ~ WT + NT + HB + SZ + YR + WT×NT + WT×HB + NT×HB + WT×SZ + NT×SZ
Growth	Spain	WT(0.84) + NT(1) + HB(1) + WT×HB(0.84) + NT×HB(1)
	Spain (LC)	WT(0.71)
	Spain (HC)	NT(1) + SZ(1)
	Sweden	WT(1) + NT(0.82) + HB(1) + SZ(1) + WT×NT(0.82) + NT×SZ(0.64)
Reproduction	Spain	WT(1) + NT(1) + SZ(1) + YR(1) + WT×NT(1) + WT×SZ(1)
	Sweden	NT(1) + SZ(1) + YR(1) + NT×SZ(0.72)
Fecundity	Spain	NT(1) + SZ(1) + YR(1) + NT×SZ(0.75)
	Sweden	WT(0.73) + NT(0.83) + HB(1) + SZ(1) + YR(1) + WT×HB(0.73) + NT×HB(0.83)
	Sweden (LC)	YR(1)
	Sweden (HC)	WT(0.81) + NT(1) + SZ(0.81) + YR(1)

Figures

Figure 1

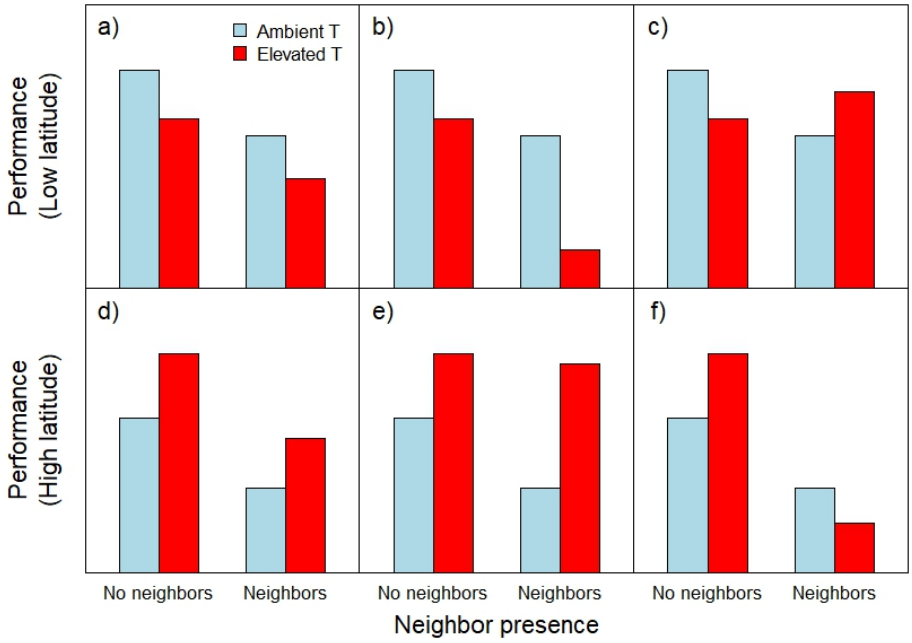


Figure 2

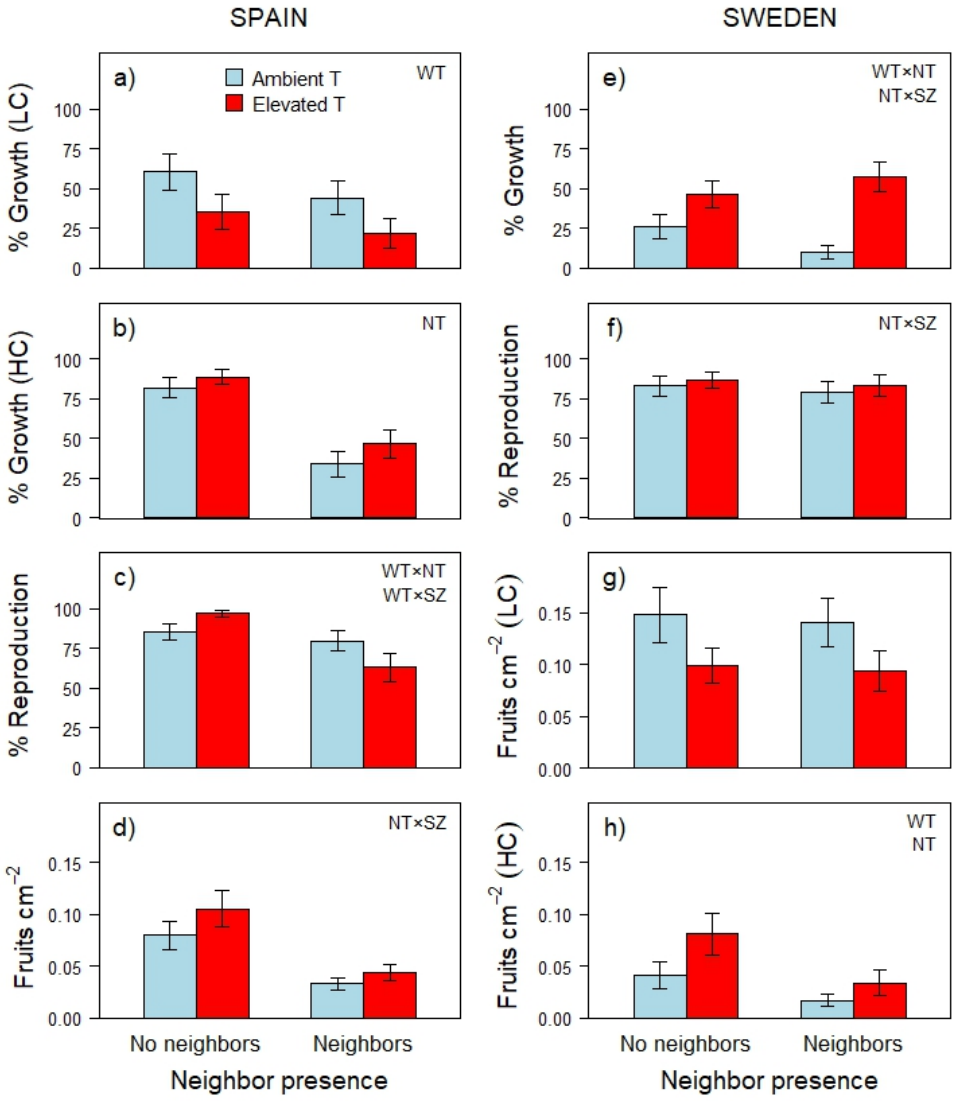
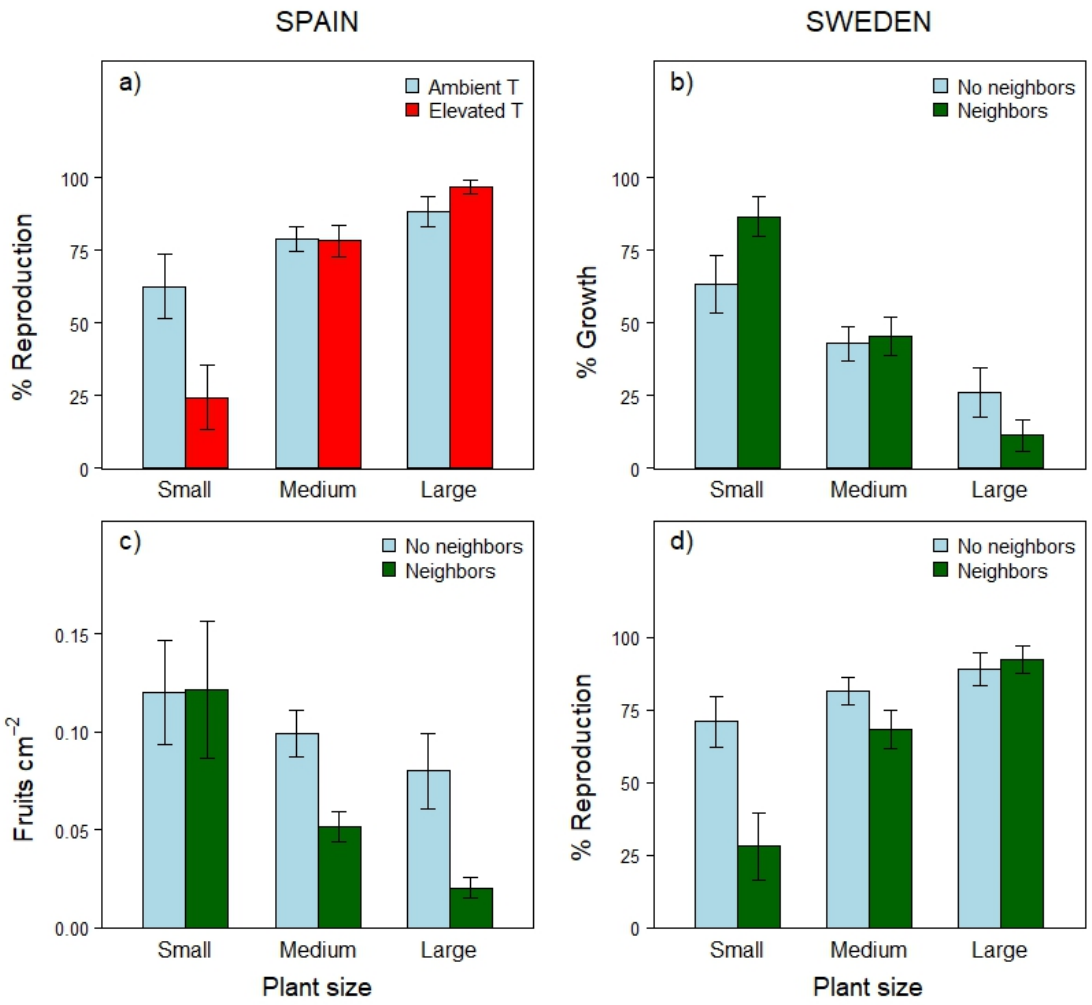

SPAIN
SWEDEN
a)
Ambient T
Elevated T
WT
% Growth (LC)
b)
NT
% Growth (HC)
c)
WT×NT
WT×SZ
% Reproduction
d)
NT×SZ
Fruits cm−2
e)
WT×NT
NT×SZ
% Growth
f)
NT×SZ
% Reproduction
g)
Fruits cm−2 (LC)
h)
WT
NT
Fruits cm−2 (HC)
No neighbors
Neighbors
Neighbor presence

Figure 3


SPAIN
SWEDEN
a)
Ambient T
Elevated T
% Reproduction
b)
No neighbors
Neighbors
% Growth
c)
Fruits cm^{-2}
d)
Small
Medium
Large
Plant size